RECONCILING TAXONOMY AND PHYLOGENY IN THE *STREPTANTHUS GLANDULOSUS* COMPLEX (BRASSICACEAE)[1]

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ABSTRACT

Previous studies have postulated that the *Streptanthus glandulosus* Hook. complex (Brassicaceae) originated through gradual range contraction and isolation of populations of an ancestral species distributed in California, United States. Here, we integrate patterns of interfertility, morphology, ITS, and chloroplast DNA (cpDNA) variation to generate a classification system reflective of the phylogeny of this group. As a result, we propose a single species, *S. glandulosus*, with 10 subspecies, to constitute the complex. Populations of *S. glandulosus* subsp. *glandulosus* distributed north of the San Francisco Bay are now divided between two new subspecies, *S. glandulosus* subsp. *arkii* M. S. Mayer and subsp. *raichei* M. S. Mayer, diagnosable through molecular apomorphies, perianth color, and fruit orientation. The name *S. peramoenus* Greene is synonymized to *S. glandulosus* subsp. *glandulosus* and is further lectotypified.

Key words: Brassicaceae, cpDNA, ITS, IUCN Red List, phylogeny, *Streptanthus*.

In the past 50 years, the *Streptanthus glandulosus* Hook. complex has received attention for a variety of reasons: bearing flowers both beautiful and atypical among crucifers (e.g., zygomorphy, connate filaments, three pairs of stamens at different heights, crisped and channeled petals), exhibiting serpentine endemism, or serving as a model for hypotheses of evolutionary divergence and speciation. Moreover, it has been recognized as a natural group, albeit diverse, since the 1890s at latest (Greene, 1904).

The group is mostly restricted to small outcrops of serpentine substrate in the California Coast Ranges, from Tehama County south to San Luis Obispo County, although a new taxon from southern Oregon has recently been described, *Streptanthus glandulosus* subsp. *josephinensis* Al-Shehbaz & M. S. Mayer (Al-Shehbaz & Mayer, 2008). Members of the complex are annuals with zygomorphic perianths featuring a colored, urceolate calyx and petals that are ± exserted and reflexed with a channeled blade and crisped, white margins. The morphological diversity among the populations, mostly in the form of perianth coloring, is bewildering. Past taxonomic schemes have recognized from one to 13 species in the group. The taxonomy currently in use recognizes three species and a number of infraspecific taxa (Table 1; Kruckeberg, 1958; Buck et al., 1993; Rollins, 1993).

In 1957, Arthur Kruckeberg published the results of a large analysis of interfertility among the populations of the complex (Kruckeberg, 1957). He found a negative correlation between the linear distance separating two populations and the fertility of their hybrids. This classic paper demonstrated that "isolation by distance" could be a potent force in the divergence and speciation of groups of populations. He used these findings to support his revision of the taxonomy of the complex (Table 1; Kruckeberg, 1958), currently used in *The Jepson Manual: Higher Plants of California* (Buck et al., 1993).

When we examined the population genetics of the *Streptanthus glandulosus* complex using enzyme electrophoresis, the same correlation emerged between geographic distance and genetic identities (Mayer et al., 1994). Subsequent phylogenetic studies of the chloroplast DNA (cpDNA) and ITS of 18S–26S nuclear ribosomal RNA genes of the group echoed and refined these patterns (Mayer & Soltis, 1994, 1999). However, we also found the present taxonomic system at odds with the phylogenetic patterns we revealed. The present study was undertaken to reconcile this conflict.

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Table 1. Comparison of taxonomic treatments for the *Streptanthus glandulosus* complex; the present study depicts *S. glandulosus* subsp. *glandulosus* sensu Kruckeberg (1958) distributed among three geographic clades depicted in Figure 1.

Kruckeberg, 1958; Buck et al., 1993; Rollins, 1993	Present classification
S. glandulosus	*S. glandulosus*
subsp. *glandulosus*	
Southern clade	subsp. *glandulosus*
Northwestern clade	subsp. *raichei*
Northeastern clade	subsp. *arkii*
subsp. *pulchellus*	subsp. *pulchellus*
subsp. *secundus*	
var. *secundus*	subsp. *secundus*
var. *sonomensis*	subsp. *sonomensis*
var. *hoffmanii*	subsp. *hoffmanii*
S. albidus	
subsp. *albidus*	subsp. *albidus*
subsp. *peramoenus*	syn., subsp. *glandulosus*
S. niger	subsp. *niger*

We have argued, as did Kruckeberg (1957), that the disjunctions among populations and the divergence among taxa of the complex were caused by vicariance rather than dispersal. The complex consists of the remnants of a widespread ancestral species, fitting the profile of a paleoendemic (Stebbins & Major, 1965). Fortunately for us, the gradual isolation of the regions within the range of the ancestral *Streptanthus glandulosus* has been marked by the concomitant accumulation of molecular apomorphies, allowing the resolution of well-supported clades in the phylogeny (Fig. 1).

Gene flow among populations within even the same variety or subspecies was estimated to be lower than is necessary to offset the effects of genetic drift (Mayer et al., 1994). Genetic variation within, and divergence among, populations is high, again supporting a vicariant rather than dispersalist history for these widely disjunct populations (Mayer et al., 1994). We suspect that as the range of the ancestral taxon fragmented over time, regions and populations were subject to genetic drift and local selection pressures, causing divergence in floral color, plant size, and pubescence while retaining varying combinations of ancestral traits. Consequently, the ancestral species served as the progenitor of multiple derived lineages throughout its range. Recognition of the group of remaining ancestral populations as a species renders it paraphyletic. Such a paraphyletic progenitor has been termed a plesiospecies and any derived species an apospecies (Olmstead, 1995), because the latter is diagnosable via apomorphies, whereas the progenitor is defined by the sharing of plesiomorphic character states. This terminology seems apt for the *Streptanthus glandulosus* complex, with its combination of rare, regional taxa and the wide-ranging, highly disjunct *S. glandulosus* subsp. *glandulosus*.

We viewed the current taxonomic structure of the *Streptanthus glandulosus* complex (Kruckeberg, 1958) as a phylogenetic hypothesis to be tested. This paper will synthesize the available data, report the results of new sequence and morphological analyses, and make taxonomic revisions that recognize the dynamic biology as well as the strong phylogenetic patterns of this species complex.

Materials and Methods

We rely largely on published data in this study. Interfertility data (Kruckeberg, 1957), cpDNA restriction site data (Mayer et al., 1994), and ITS sequences (Mayer & Soltis, 1999) are reviewed and, in some cases, regenerated or augmented by the addition of new populations and data.

POPULATION SAMPLING

The present study refers to populations analyzed by Kruckeberg (1957) and to populations studied in the cpDNA study (Mayer & Soltis, 1994), which attempted to sample, as close as possible, exemplars of the same populations as the Kruckeberg study. If these populations could not be located or no longer existed, we sampled others that were relatively near. DNA of three to seven plants per population was pooled for the molecular work (Mayer & Soltis, 1994). The 29 populations (Appendix 1) represented here provide a good sample of the taxa and geographic regions in the range of the complex (Fig. 1). We used *Streptanthus polygaloides* A. Gray as the outgroup for the analyses, as it had been successfully used for this purpose in earlier analyses (Mayer & Soltis, 1999).

MORPHOLOGICAL STUDY

We examined herbarium specimens of wild and greenhouse-grown plants to look for morphological patterns to compare with molecular phylogenetic patterns. Because flower color is not preserved well in herbarium specimens but carries significant weight in the diagnostic keys and species descriptions, we photographed the flowers of plants grown in the greenhouse from wild-collected seed. Nearly all populations are represented in this way. We examined the collections of the following herbaria through loans or visits: CAS, CHSC, DS, JEPS, OBI, RSA, SD, and UC.

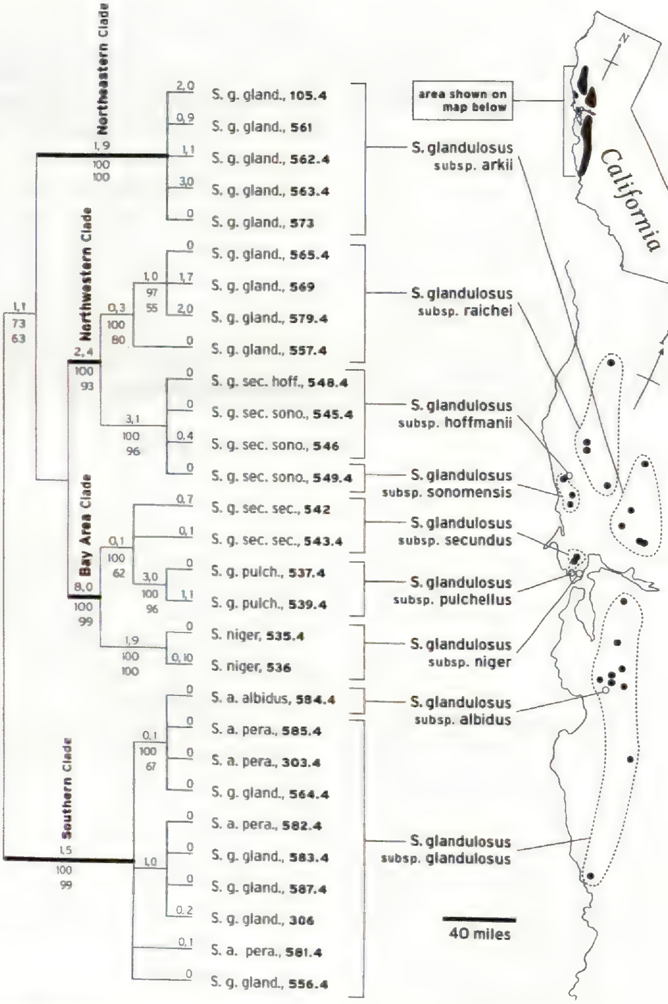

Figure 1. Strict consensus tree of relationships among populations of the *Streptanthus glandulosus* complex in California, compared with biogeography and taxonomic treatments. Clade terminals are identified by the traditional taxonomic treatment (Kruckeberg, 1958) and collection number (Appendix 1) on the left and by the present taxonomic treatment (Table 1) on the right, which is also related to geographic origin on the map. The traditional nomenclature is abbreviated as follows: a., *albidus*; g. or gland., *glandulosus*; hoff., *hoffmanii*; pera., *peramoenus*; pulch., *pulchellus*; sec., *secundus*; sono., *sonomensis*. Branch lengths are noted above branches (separately for restriction site and ITS apomorphies, respectively); Bayesian posterior probabilities are noted above bootstrap values below branches. The tree is rooted by *S. polygaloides* (not shown), which had a branch length of 42.

MOLECULAR DATA

cpDNA restriction site data were generated by the study of Mayer et al. (1994), which assessed variation at 948 sites (ca. 3.6%) of the genome. ITS amplification and sequencing undertaken by the present study followed the methods of Mayer and Soltis (1999), with the exception that ITS amplification products were purified using the GFX PCR Purification kit (Amersham Pharmacia Biotech, Piscataway, New Jersey, U.S.A.). Purified products were subjected to automated sequencing using ABI 377 technology (Applied Biosystems, Foster City, California, U.S.A.) at the San Diego State University Microchemical Core Facility. Of the 29 ITS sequences of the complex analyzed herein (Appendix 1), 24 are new or have not been previously analyzed (12 of these from populations not analyzed in previous studies) and five were analyzed previously (Mayer & Soltis, 1999). The combined data matrix for all 29 populations consists of 35 variable cpDNA restriction sites (excluding apomorphies on the branch leading to the outgroup) plus the alignment of ITS-1 and ITS-2 sequences, which provides 62 variable positions within the complex.

PHYLOGENETIC ANALYSES

Sequences were aligned visually and were subjected to maximum parsimony analysis (with tree bisection-reconnection [TBR] branch swapping) and bootstrap analysis (1000 replicates) by PAUP* 4.0b10 (Swofford, 2001). Bayesian analysis employed the general time reversible (GTR) DNA substitution model option of MrBayes 3.0 (Huelsenbeck & Ronquist, 2001), the model preferred by Modeltest 3.6 (Posada & Crandall, 1998). Four rate categories were set for the gamma distribution. MrBayes ran four simultaneous Monte Carlo chains for 1,000,000 generations, saving trees every 100 generations, but discarding the first 1000 trees (burn-in value) prior to constructing the consensus tree.

RESULTS AND DISCUSSION

PHYLOGENETIC PATTERNS

The combined analysis of cpDNA and ITS sequence data reveals a robust pattern of relationships among the populations of the *Streptanthus glandulosus* complex (Fig. 1). The major clades are well supported and geographically structured. This phylogenetic pattern, however, does not correspond well with Kruckeberg's (1958) taxonomy for the complex (Fig. 1). Although Kruckeberg's (1957) patterns of interfertility among populations of the complex were strongly correlated with geographic distance, the taxonomic structure he used (1958) was not. Consequently, the interfertility patterns show greater congruence with clade membership than with taxonomy (Table 2). For example, populations of Kruckeberg's *S. glandulosus* subsp. *glandulosus* north of the San Francisco Bay proved to be closer phylogenetically to any population of any other taxon endemic to this region than to populations of subspecies *glandulosus* east or south of the bay (Fig. 1). Interfertility among populations north versus populations east and south of the bay displays the same pattern: average interfertilty is better predicted by geographic proximity of populations than by taxonomic affiliation (Table 2).

The clade-based analysis of Kruckeberg's taxa and interfertility (Table 2) depicts populations of *Streptanthus glandulosus* subsp. *glandulosus* from east and south of the San Francisco Bay on a well-supported clade encompassing all of the populations of Kruckeberg's *S. albidus* Greene subsp. *albidus* and subsp. *peramoenus* (Greene) Kruckeb. (Fig. 1). Also, popula-

Table 2. Mean interfertility among populations of the *Streptanthus glandulosus* complex.*

	S. albidus	*S. niger*	*S. gland.* subsp. *gland.* S	*S. gland.* subsp. *gland.* NW	*S. gland.* subsp. *gland.* NE	*S. gland.* subsp. *pulch.*	*S. gland.* subsp. *sec.* var. *sec.*	*S. gland.* subsp. *sec.* var. *sono.*
S. albidus	86.3 (12, 16.3)							
S. niger	17.5 (4, 22.2)	no data						
S. gland. subsp. *gland.* S	10.0 (5, 13.7)	5.0 (2, 7.1)	5.0 (1, 0)					
S. gland. subsp. *gland.* NW	0.3 (15, 1.3)	10.0 (3, 0)	3.6 (7, 6.3)	87.8 (16, 24.2)				
S. gland. subsp. *gland.* NE	5.0 (3, 5.0)	0 (1, 0)	0 (2, 0)	62.1 (7, 44.9)	51.00 (5, 47.0)			
S. gland. subsp. *pulch.*	0 (8, 0)	0 (1, 0)	5.0 (3, 8.7)	54.5 (11, 16.4)	no data	100 (1, 0)		
S. gland. subsp. *sec.* var. *sec.*	0 (6, 0)	0 (1, 0)	0 (1, 0)	58.3 (3, 7.6)	75.0 (1, 0)	95.8 (6, 2.0)	90.0 (2, 7.1)	
S. gland. subsp. *sec.* var. *sono.*	0 (12, 0)	6.3 (4, 9.5)	17.0 (5, 38.0)	87.9 (26, 18.6)	41.0 (10, 43.5)	71.7 (18, 18.4)	68.5 (23, 21.2)	93.2 (28, 7.7)

* Data from Kruckeberg (1957) are partitioned and summarized to make comparisons between taxa and clades (see Table 1). Each cell shows mean percent viability of F1 pollen, and the number of crosses involved followed by the standard deviation of the mean are in parentheses. Comparisons for which no crosses were made are designated "no data." Abbreviations: gland., *glandulosus*; pulch., *pulchellus*; sec., *secundus*; sono., *sonomensis*; S, NW, NE, Southern, Northwestern, Northeastern clades, respectively (see Fig. 1).

tions of *S. glandulosus* subsp. *glandulosus* from northwest of the bay (the Northwestern [NW] clade, Fig. 1) showed higher interfertility with the varieties of *S. glandulosus* subsp. *secundus* (Greene) Kruckeb. of that region (variety *secundus* = 75.0%, variety *sonomensis* Kruckeb. = 93.0%; Table 2) than with subspecies *glandulosus* from the southern counties (1.9%). Similarly, the two geographically proximate varieties of subspecies *secundus* (varieties *secundus* and *sonomensis*) had relatively low interfertility in the crossing study (68.5%), and in the molecular phylogeny it is clear that they are not sister taxa: variety *secundus* is sister to *S. glandulosus* subsp. *pulchellus* (Greene) Kruckeb. (interfertility = 95.8%) and variety *sonomensis* is sister to subspecies *glandulosus* of the NW clade (interfertility = 93.0%, Fig. 1). Overall, most of the cases of low or high interfertility that were surprising in the context of the crossing study are not unexpected given the topology of the molecular phylogenies; they simply signify cases of disconnect between taxonomy and phylogeny of the group.

Synthesis of the patterns of topology, geography, and morphology constitutes compelling evidence for the paleoendemic history of this lineage. *Streptanthus glandulosus* subsp. *glandulosus* is highly paraphyletic and serves as a vivid example of a plesiospecies that has given rise to multiple narrow endemics. Because this taxon is distributed among three robust, geographically structured clades of the molecular phylogeny (i.e., the Southern, NW, and NE clades, Fig. 1), we checked for morphological apomorphies that might also mark these clades and discuss them in turn below.

This shared history of *Streptanthus albidus* subsp. *peramoenus* and populations of *S. glandulosus* subsp. *glandulosus* east and south of the San Francisco Bay is suggested by morphological as well as molecular data. Flower color of subspecies *glandulosus* from this region varies from lavender and violet, which it shares with subspecies *peramoenus*, to dark maroon. The molecular phylogeny depicts both subspecies of *S. albidus* and all these populations of subspecies *glandulosus* on the same well-supported clade, which we call the Southern clade (Fig. 1). The molecular divergence among members of this clade is minor, and several populations of the three taxa are indistinguishable using the ITS and cpDNA data. Examination of specimens, including greenhouse grown, of subspecies *glandulosus* from north of the bay versus those of the Southern clade (n = 82 and 87, respectively, unpublished data not shown), as well as *S. albidus* subsp. *peramoenus* (n = 40, unpublished data not shown) showed a combination of non-perianth features that align the southern subspecies *glandulosus* with *S. albidus* rather than with northern subspecies *glandulosus*. There is generally less pubescence in the Southern clade of subspecies *glandulosus* than in the northern clades, but the clearest distinction is seen in the shape of the mid- to upper-cauline leaves. In both *S. albidus* and southern subspecies *glandulosus*, these leaves are narrow, often folded and grasslike, and entire or with few, minute teeth. The northern clades of subspecies *glandulosus* typically exhibit broader leaves with small to large lobelike teeth. There is a greater similarity in average midcauline leaf length:width ratio of southern subspecies *glandulosus* (16.45, standard deviation [SD] = 9.31) to that of subspecies *peramoenus* (19.75, SD = 7.81) than to that of subspecies *glandulosus* north of the bay (NW clade: 4.40, SD = 2.51, n = 42; NE clade: 8.32, SD = 11.62, n = 40). Thus, despite perianth color similarity between some of the southern subspecies *glandulosus* and northern subspecies *glandulosus*, the Southern clade still can be diagnosed morphologically. On the other hand, *S. albidus* subsp. *albidus*, with its white to cream-colored perianth, is easily distinguished from the other taxa of the Southern clade even though it also lacks any observed molecular divergence from these taxa (Fig. 1).

The NW and NE clades of *Streptanthus glandulosus* subsp. *glandulosus*, which are geographically contiguous, are clearly resolved by a combination of congruent cpDNA and ITS apomorphies (Fig. 1). Enzyme electrophoretic data exhibited a similar pattern of differentiation (Mayer et al., 1994). Kruckeberg (1957) informally recognized similar geographically based groups north of the San Francisco Bay: his North Coast group with rose-colored flowers in Sonoma and Mendocino counties, and his North Interior group with dark purple to blackish flowers found in the inner Coast Range regions to the east. Our molecular analyses indicate that Kruckeberg's North Interior group is actually split between the NW and NE clades we have identified (Fig. 1).

Although the nuances of perianth color can be lost in dried specimens, plants of the NW and NE clades can be distinguished by fruit orientation, a feature that has not been previously linked to geography or taxonomy within the *Streptanthus glandulosus* complex. Populations of the NW clade bear fruits that are recurved to reflexed at maturity, whereas those of the NE clade are ascending to erect. In both clades, the fruits themselves are straight to slightly curved, so the differences between the clades are primarily due to pedicel orientation. Additional morphological patterns that coincide with the molecular-based clades include a modification of Kruckeberg's trends: the perianth colors of the NW clade include not only rose-pink, but deeper shades of magenta to maroon on the sepals and petals. The darker shades can be found following veins of the petals or as solid coloring of the petals and parts of the sepals. Sepal color is most intense basally; the keel and tip of the sepals retain some green color at full anthesis. Flowers of the NE clade, however, exhibit a dark maroon-brown to blackish color on sepals and petals, and there is usually no visible green on the sepals at full anthesis. Identifying the perianth color differences between the NW and NE clades is difficult on dried specimens, which tend to lose the red and green perianth pigments and exhibit just shades of purple, brown, and straw. Finally, the leaves of the NW clade tend to be somewhat shorter and broader on average than those of the NE clade: means of midcauline leaf length:width are 4.40 (SD = 2.51, n = 42) and 8.32 (SD = 11.62, n = 40), respectively.

The NW clade also gave rise to what Kruckeberg (1958) recognized as two varieties of *Streptanthus glandulosus* subsp. *secundus*, as variety *sonomensis* and variety *hoffmanii* Kruckeb. (Fig. 1). This relationship is well supported on the molecular phylogeny and entirely consistent with geographical patterns; variety *hoffmanii* is found in just a few populations on the northern edge of the distribution of variety *sonomensis*. As mentioned above, variety *sonomensis* showed higher interfertility with nearby populations of subspecies *glandulosus* than it did with the type variety of subspecies *secundus* (Kruckeberg, 1957; Table 2). Its greenish white to yellow perianth color, however, renders it morphologically distinct from both taxa. At the time of the interfertility study, variety *hoffmanii* had not yet been described, so specific interfertility data are not available for it. It is, however, almost indistinguishable from variety *sonomensis* and nearby populations of subspecies *glandulosus* in allozymic, cpDNA, and ITS sequence profiles. Morphologically, it can be similar to subspecies *glandulosus* of the region, with a perianth colored rose to magenta. It is distinct, however, in its secund inflorescences.

The Bay Area clade portrays *Streptanthus niger* Greene as sister to a clade bearing *S. glandulosus* subsp. *pulchellus* and *S. glandulosus* var. *secundus* (Fig. 1). The latter two taxa are found less than 10 km from each other and exhibit high interfertility (95.83%, Table 2). *Streptanthus niger*, which consists of just two populations on the Tiburon Peninsula in the San Francisco Bay, is distinguished by eight molecular apomorphies and a few morphological traits: an often flexuose raceme rachis, a highly constricted corolla throat, and a glabrous surface throughout. It also exhibits self-pollination and a greatly depressed interfertility with the other taxa of the complex. The combination of these features was used as justification for species-level recognition for this taxon in Kruckeberg's revision (1958). Indeed, most crosses of any taxon with *S. niger* lead to a sterile F1, but a few progeny did show fertility up to 10% (variety *glandulosus*), 20% (variety *sonomensis*), and 50% (*S. albidus*; Kruckeberg, 1957).

In his study of interfertility, Kruckeberg (1957) set out to quantify the effect of geographic isolation on genetic divergence of populations; he developed an elegant and sturdy model of vicariance and diversification in the complex. His subsequent revision of taxonomy (1958) was pragmatic but includes paraphyletic taxa. We now propose a taxonomic revision in which named taxa are both compatible with phylogenetic relationships and are morphologically diagnosable.

REVISED CLASSIFICATION OF THE *STREPTANTHUS GLANDULOSUS* COMPLEX

The proposed taxonomic system recognizes both the shared ancestry of the *Streptanthus glandulosus* complex as well as the distinct lineages within it. The complex consists of a single species, *S. glandulosus*, comprising 10 subspecies. These taxa generally exhibit levels of morphological, geographic, and genetic divergence greater than those suggested for the rank of variety (Stuessy, 1990), but less than what may be warranted for the rank of species.

Of the current subspecies of *Streptanthus glandulosus*, two are maintained and exhibit morphological and geographical distinction, as subspecies *pulchellus* and subspecies *secundus*. Two other varieties considered by Kruckeberg in 1958 for subspecies *secundus* are not closely related to its type but are morphologically and geographically distinct. They were recently elevated to subspecies, as *S. glandulosus* subsp. *sonomensis* (Kruckeb.) M. S. Mayer & D. W. Taylor and *S. glandulosus* subsp. *hoffmanii* (Kruckeb.) M. S. Mayer & D. W. Taylor (Al-Shehbaz & Mayer, 2008). The previous taxonomic concept of *S. glandulosus* subsp. *glandulosus* included the three robust lineages of the Southern, NW, and NE clades in California, all of which merit recognition at the level of subspecies. The type of *S. glandulosus* was collected in Monterey and exhibits morphology most consistent with that of the Southern clade, and new subspecific epithets are proposed for the remaining two clades (Table 1).

The morphological distinction of the taxon *albidus*, first recognized as *Streptanthus albidus* Greene (Greene, 1887), is maintained herein, transferred as subspecies *albidus* within *S. glandulosus* (Al-Shehbaz & Mayer, 2008). Kruckeberg (1958) reduced another species of Greene (1887) as subspecies *peramoenus* (Greene) Kruckeberg. However, this intergrades morphologically with subspecies *glandulosus* and is largely indistinguishable in the molecular data set

(Fig. 1). *Streptanthus peramoenus* is therefore synonymized under *S. glandulosus* subsp. *glandulosus*.

Finally, *Streptanthus niger* was recognized as a subspecies and transferred to *S. glandulosus* (Al-Shehbaz & Mayer, 2008). It is distinct at the molecular level (Fig. 1) and is largely intersterile (but not entirely) with most other populations of the complex (Table 2). Although these features might constitute a rationale for species-level recognition, similar levels of intersterility and molecular distinction may be found in other populations of the complex (Kruckeberg, 1957; Mayer & Soltis, 1999). Moreover, crosses between *S. niger* and its nearest relatives (*S. glandulosus* subsp. *pulchellus* and subsp. *secundus*) were very few in number (Table 2), leaving those measures weakly supported.

Because human-mediated and possibly natural processes continue to eliminate populations of the *Streptanthus glandulosus* complex, geographic isolation among surviving populations of even the narrowest endemic is likely to increase over time. This prediction, coupled with the low level of gene flow already present among populations of the complex, suggests that, phylogenetically, this complex consists of numerous incipient species. However, we feel that recognition of the *S. glandulosus* complex as diverging scions of the paleoendemic *S. glandulosus* best conveys the cohesive but dynamic nature of this species complex, which understandably might defy adequate representation by a static taxonomic structure.

TAXONOMIC TREATMENT

1. **Streptanthus glandulosus** Hook., Icon. Pl. 1, pl. 40. 1836. *Erysimum glandulosum* (Hook.) Kuntze, Rev. Gen. 2: 933. 1891. *Euklisia glandulosa* (Hook.) Greene, Leafl. Bot. Observ. Crit. 1: 82. 1904, as "*Euclisia*." TYPE: U.S.A. California: Monterey Co., Monterey, 1833, *D. Douglas s.n.* (holotype, K not seen; isotypes, GH not seen, MO!).

Annual; stems erect, 1–12 dm, simple or divaricately branched just above the basal rosette, glabrous (and glaucous in some) to sparingly (rarely densely) hispid to the inflorescence, plants densely rosulate at first, basal leaves 5–12 cm, hispid, narrowly lanceolate, tapering to a short, winged petiole, coarsely and sinuately toothed to shallowly pinnatifid, the teeth callus-tipped; cauline leaves sessile, auriculate, narrowly oblanceolate, coarsely dentate to ± lobed, gradually reduced upward, becoming sessile, auriculate, lanceolate-acuminate to linear and conduplicate, entire to ± lobed; by anthesis basal and lower cauline leaves becoming deciduous and stems ultimately naked up to 2 or 3 nodes below the inflorescence. Flowers ascending to erect or secund, in single to several open erect racemes, some rachises flexuose; at anthesis flowers on pedicels 1–2 cm, spaced at intervals of 2–4 cm from base to apex. Calyx urceolate, sepals 4–9 mm, oval, glabrous or sparingly hispid, wholly or partly connivent, and strongly keeled; petals 6–15 mm, bilateral and barely to well exserted, the crisped margins usually white, the adaxial pair with broad blades, slightly to strongly recurved, longer than the abaxial, less recurved and narrower pair; stamens in 3 pairs, the adaxial with filaments connate to 0.5–0.75 their length, bearing sterile or scarcely polliniferous anthers, the abaxial and lateral pair fertile, extending and dehiscing in that order, scarcely exserted. Siliques glabrous (or rarely hispid), not torulose, 5–8 cm, straight and ascending or divaricate, to arcuate and descending to reflexed; seeds oblong-oval, winged, 2–2.5 × 1–1.5 mm; cotyledons accumbent.

KEY TO THE SUBSPECIES OF *STREPTANTHUS GLANDULOSUS* IN CALIFORNIA AND SOUTHERN OREGON, U.S.A.

1a. Plants entirely glabrous; inflorescence rachises flexuose; pedicels longer than the flowers; petals barely (2–3 mm) exserted and not recurved; Tiburon Peninsula, Marin Co. . . . . 1f. *S. glandulosus* subsp. *niger* (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor

1b. Plants sparsely hairy to hispid; inflorescence rachises ± straight; pedicels shorter than the flowers; petals generally well (> 5 mm) exserted and recurved.

2a. Inflorescences secund or nearly so.

3a. Sepals white, cream, greenish white, or pale yellow.

4a. Perianth cream to light greenish yellow with rose or lavender-purple on sepal base or petal veins.

5a. Petals 7–8 mm; fruits divaricate-ascending, straight or curved inward; Josephine Co., Oregon . . . . 1e. *S. glandulosus* subsp. *josephinensis* Al-Shehbaz & M. S. Mayer

5b. Petals 10–17 mm; fruits spreading to reflexed, arcuate; north slope of Mt. Tamalpais and nearby Marin Co. . . . . 1i. *S. glandulosus* subsp. *secundus* (Greene) Kruckeb.

4b. Perianth greenish white to yellow, without purplish or lavender base; petals without purple veins; Sonoma Co. . . . . 1j. *S. glandulosus* subsp. *sonomensis* (Kruckeb.) M. S. Mayer & D. W. Taylor

3b. Sepals rose to reddish purple.

6a. Perianth entirely rose to magenta; fruiting pedicels 5–15 mm; fruits arcuate, spreading to reflexed; Sonoma Co. . . . . 1d. *S. glandulosus* subsp. *hoffmanii* (Kruckeb.) M. S. Mayer & D. W. Taylor

6b. Perianth red to reddish purple; fruiting pedicels 2–5 mm, fruits curved upward, divaricate to ascending; Marin Co. . . . . 1g. *S. glandulosus* subsp. *pulchellus* (Greene) Kruckeb.
2b. Inflorescences not secund.
7a. Plants 5–12 dm, glaucous and nearly glabrous; perianth cream to greenish white, with purple tinge at base of sepals; rare, Santa Clara Co. . . . . 1a. *S. glandulosus* subsp. *albidus* (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor
7b. Plants 2–10 dm, surfaces variable; perianth rose-magenta, violet, or dark maroon to black.
8a. Fruits recurved to reflexed . . . . 1h. *S. glandulosus* subsp. *raichei* M. S. Mayer
8b. Fruits ascending to erect.
9a. Plants 2–10 dm; midcauline leaves linear and conduplicate (length usually greater than 10× width), margin entire or with few minute teeth; perianth lilac-lavender to dark violet (rarely maroon); Coast Ranges: Contra Costa Co. south to San Luis Obispo Co. . . . . 1c. *S. glandulosus* Hook. subsp. *glandulosus*
9b. Plants 2–7 dm; midcauline leaves oblanceolate and flat to conduplicate (length usually less than 5× width), margin usually with small to large lobelike teeth; perianth maroon to blackish (rarely dark violet); Colusa, Lake, Napa, Solano, Tehama, and eastern Sonoma counties . . . . 1b. *S. glandulosus* subsp. *arkii* M. S. Mayer

1a. Streptanthus glandulosus subsp. **albidus** (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus albidus* Greene, Pittonia 1: 62. 1887. *Euklisia albida* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia.*" *Streptanthus glandulosus* var. *albidus* (Greene) Jeps., Man. Fl. Pl. Calif. 419. 1925. TYPE: U.S.A. California: Santa Clara Co., hillsides 4 mi. S of San Jose, 30 Apr. 1887, *Rattan s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *albidus* is rare, possibly limited to serpentine substrate in Metcalf Canyon in the Mount Hamilton range in Santa Clara County, California (Appendix 1).

Discussion. Plants of *Streptanthus glandulosus* subsp. *albidus* are among the tallest in the complex (5–12 dm) and are glaucous and nearly glabrous. The perianth is cream to greenish white, with a purple tinge at the sepal base.

1b. Streptanthus glandulosus subsp. **arkii** M. S. Mayer, subsp. nov. TYPE: U.S.A. California: Napa Co., SE slope of Mt. St. Helena, 1946, *L. Constance, J. F. Davidson, H. W. Wagner & R. H. Shan 3049* (holotype, UC!).

Haec subspecies *Streptantho glanduloso* Hook. subsp. *glanduloso* similis, sed ab eo foliis mediocaulinis minus quam 5plo longioribus quam latioribus, perianthio atrorubropurpureo usque nigello, sepalis sub anthesi plerumque non viridibus et siliquis ascendentibus usque erectis distinguitur.

Plants 2–7 dm, sparsely hairy to hispid. Midcauline leaves oblanceolate and flat to conduplicate, length less than 5× the width, margins usually with small to large lobelike teeth. Inflorescences not secund, rachises ± straight, pedicels shorter than the flowers. Perianth colors range from dark maroon to blackish (rarely dark violet), usually with no visible green on the sepals at full anthesis. Fruits are ascending to erect.

Distribution and habitat. *Streptanthus glandulosus* subsp. *arkii* has been collected from Colusa, Napa, Lake, Solano, and Tehama counties and the eastern edge of Sonoma County in California on outcrops of broken and decomposed serpentine, serpentine grasslands, and roadcuts through serpentine and nonserpentine substrate (Appendix 1).

IUCN Red List category. *Streptanthus glandulosus* subsp. *arkii* is Vulnerable (VU C2a[i]) according to IUCN Red List criteria (IUCN, 2001). In our assessment, *S. glandulosus* subsp. *arkii* is uncommon, exists in isolated populations, and is vulnerable to pressures from habitat degradation and urbanization.

Discussion. *Streptanthus glandulosus* subsp. *arkii* is similar to *S. glandulosus* subsp. *glandulosus* except that the length of midcauline leaves is less than 5× the width and the margins usually have small to large lobelike teeth. Perianth colors, from dark maroon to blackish (rarely dark violet), are darker than the range of subspecies *raichei*, and fruits of subspecies *arkii* are ascending to erect, whereas those of subspecies *raichei* are recurved to reflexed.

Etymology. The subspecific epithet honors Arthur R. Kruckeberg (1920–), a groundbreaking researcher in the evolution and ecology of serpentine plants and a generous benefactor of the present project.

Paratypes. U.S.A. **California:** Colusa Co., ridge betw. Venado & Leesville, 1938, *Hoover 3227* (UC); Lake Co., 3.1 mi. S of Middletown jct. on Peterson Ranch Rd., Dog Rock, 1948, *Hoffman 2333* (UC); Napa Co., burn below Conn Dam, 1951, *P. Raven 2825* (UC); below Samuel Springs along Pope Creek on rd. from Monticello, 1941, *R. F. Hoover 4912* (UC); Solano Co., Vaca Mtns., Walker Cyn., N fork of canyon, *W. L. Jepson 13410* (JEPS); Sonoma Co., at the Geysers, 1864, *H. N. Bolander 3944* (UC); Tehama Co., N of Paskenta, Colyear Springs Rd., 0.8 mi. W of Lowery Rd., 1991, *V. H. Oswald & L. Ahart 4498* (UC).

1c. Streptanthus glandulosus Hook. subsp. **glandulosus**, Icon. Pl. 1, pl. 40. 1836. *Streptanthus peramoenus* Greene, Bull. Torrey Bot. Club 13: 142. 1886, as "*peramaenus*," syn. nov. *Streptanthus albidus* Greene subsp. *peramoenus* (Greene) Kruckeb., Madroño 14: 225. 1958. TYPE: U.S.A. California: Contra Costa Co., Oakland Hills, 25 May 1886, *E. L. Greene s.n.* (lectotype, designated here, NDG not seen; duplicates, CAS not seen, GH not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *glandulosus* is uncommon, found mostly on serpentine, in grasslands, rocky slopes, and open woodland of the Coast Ranges from Contra Costa County south to San Luis Obispo County in California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *glandulosus* is 2–10 dm tall, depending on site conditions. The midcauline leaves are linear and conduplicate, and the length is usually 10× the width, with margins entire or with few minute teeth. The perianth is lilac-lavender to blackish purple with little to no green on the mature calyx. The fruits are ascending to erect.

Kruckeberg failed to locate the specimen cited above and in 1958 lectotypified a specimen collected by H. N. Bolander (*H. N. Bolander s.n.*) without stating a herbarium of deposit. Later, in 1970, he examined and annotated the Greene specimen above as the type. The location of the Bolander specimen is currently unknown.

Greene's protologue (1886: 142) mentions two specimens: "Oakland Hills; collected many years ago by Mr. Bolander, and again this year, by the writer." Of these syntypes, Barbara Hellenthal at NDG (pers. comm.) did confirm Kruckeberg's later annotation ("Feb. 1970") as type on NDG 01877. Ihsan Al-Shehbaz (pers. comm.) further considered the *Greene s.n.* collection and the NDG sheet to represent the lectotype for the name, with isolectotypes seen by him at CAS and GH. Here, we maintain his opinion and designate the NDG specimen as lectotype.

1d. Streptanthus glandulosus subsp. **hoffmanii** (Kruckeb.) M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus glandulosus* var. *hoffmanii* Kruckeb., Madroño 14: 223. 1958. TYPE: U.S.A. California: Sonoma Co., Russian Gulch, 8 mi. S of Ft. Ross, moist soil of steep, rocky, nonserpentinized bank, 400 ft., 24 Apr. 1938, *L. Constance 2155* (holotype, UC!; isotypes, GH not seen, MO!).

Distribution and habitat. Plants of *Streptanthus glandulosus* subsp. *hoffmanii* are rare, known from a few populations on serpentine and non-serpentine substrate in the Russian Gulch and Austin Creek regions north of the Russian River in Sonoma County, California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *hoffmanii* differs from *S. glandulosus* subsp. *raichei*, which also occurs in Sonoma County, by secund inflorescences and a lighter rose to magenta perianth color. Fruiting pedicels are 5–15 mm, and fruits are curved down, spreading to reflexed.

1e. Streptanthus glandulosus subsp. **josephinensis** Al-Shehbaz & M. S. Mayer, Novon 18: 280. 2008. TYPE: U.S.A. Oregon: Josephine Co., serpentine soil 6.9 mi. N of California–Oregon line on Happy Camp–O'Brien rd., 9 July 1948, *F. W. Hoffman 2311* (holotype, MO!; isotypes, GH not seen, UC!).

Distribution and habitat. *Streptanthus glandulosus* subsp. *josephinensis* has been collected only a few times on serpentine substrate around the type locality in Josephine County, Oregon.

Discussion. *Streptanthus glandulosus* subsp. *josephinensis* shares with *S. glandulosus* subsp. *secundus* secund inflorescences and a cream perianth color, but flowers of subspecies *josephinensis* produce petals 7–8 mm long and divaricate-ascending fruit, whereas the petals of subspecies *secundus* are 10–17 mm and the fruit is spreading to reflexed.

1f. Streptanthus glandulosus subsp. **niger** (Greene) Al-Shehbaz, M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus niger* Greene, Bull. Torrey Bot. Club 13: 141. 1886. *Euklisia nigra* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." *Streptanthus glandulosus* var. *niger* (Greene) Munz, Aliso 4: 91. 1958. TYPE: U.S.A. California: Marin Co., Point Tiburon, Apr. 1886, *E. L. Greene s.n.* (lectotype, NDG not seen).

Distribution and habitat. A rare taxon, *Streptanthus glandulosus* subsp. *niger* is known to exist only in one area of serpentine grassland on the Tiburon Peninsula, in Marin County, California (Appendix 1).

Discussion. *Streptanthus glandulosus* subsp. *niger* is glabrous and produces flexuose racemes with dark maroon to black sepals; the petals are barely (2–3 mm) exserted and colored the same as the sepals but with crisped white margins; and the pedicels exceed the length of the flowers.

1g. Streptanthus glandulosus subsp. **pulchellus** (Greene) Kruckeb., Madroño 14: 222. 1958. Basionym: *Streptanthus pulchellus* Greene, Pittonia 2: 225. 1892. *Euklisia pulchella* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." *Streptanthus glandulosus* var. *pulchellus* (Greene) Jeps., Man. Fl. Pl. Calif. 420. 1925. TYPE: U.S.A. California: Marin Co., dry ridges on the S flank of Mt. Tamalpais, 7 May 1892, *M. A. Howe s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *pulchellus* is rare, found only on serpentine substrate on Mount Tamalpais in Marin County, California (Appendix 1).

Discussion. Plants of *Streptanthus glandulosus* subsp. *pulchellus* are 1–3 dm, among the shortest in the complex. The subspecies has a crowded, sometimes secund inflorescence of red to reddish purple flowers, contrasting sharply with *S. glandulosus* subsp. *secundus*, which also occurs in Marin County, but has cream to pale greenish yellow flowers.

1h. Streptanthus glandulosus subsp. **raichei** M. S. Mayer, subsp. nov. TYPE: U.S.A. California: Mendocino Co., Ukiah, 27 May 1905, *W. L. Jepson 2508A* (holotype, JEPS!).

Haec subspecies *Streptantho glanduloso* Hook. subsp. *glanduloso* similis, sed ab eo foliis mediocaulinis minus quam 5plo longioribus quam latioribus, perianthio roseo usque rubropurpureo vel colore fuscato tincto secus venas petalorum, sepalis ad basim intensissime coloratis ad carinam apicesque sub anthesi colorem viridem aliquam retinentibus et siliquis recurvis usque reflexis distinguitur.

Plants 2–10 dm, sparsely hairy to hispid. Length of midcauline leaves less than 5× the width. Inflorescence not secund, rachises ± straight, pedicels shorter than the flowers. Perianth color ranges from rose-magenta to purple (rarely maroon), either fully or with darker shades following petal veins; sepal color is most intense basally, the keel and tip of the sepals usually retain some green color at full anthesis. Fruits are recurved to reflexed.

Distribution and habitat. *Streptanthus glandulosus* subsp. *raichei* has been collected from Lake, Mendocino, and northeastern Sonoma counties in California on outcrops of broken and decomposed serpentine, serpentine grasslands, and roadcuts through serpentine and non-serpentine substrate (Appendix 1).

IUCN Red List category. *Streptanthus glandulosus* subsp. *raichei* is Vulnerable (VU C2a[i]) by IUCN Red List (2001) criteria. In our assessment, this taxon is uncommon, exists in isolated populations, and is vulnerable to pressures from habitat degradation and urbanization.

Etymology. The subspecific epithet honors Roger Raiche (1952–), an excellent field botanist and great asset to our understanding of *Streptanthus* in California.

Discussion. *Streptanthus glandulosus* subsp. *raichei* is similar to *S. glandulosus* subsp. *glandulosus* except that the length of midcauline leaves is less than 5× the width, rather than greater. Subspecies *raichei* lacks the fully secund inflorescenses typical of subspecies *hoffmanii*, which is rare but also found in Sonoma County. The fruits are recurved to reflexed, which distinguishes this subspecies from *S. glandulosus* subsp. *arkii*.

Paratypes. U.S.A. **California:** Lake Co., Highland Creek, 1948, *F. W. Hoffman 2336* (UC); Mendocino Co., Ukiah, head of S Mill Creek, 1921, *W. L. Jepson 9223* (JEPS); Sonoma Co., roadcut along Pine Flat Rd., 12.1 km N of Hwy. 128, 1991, *M. Mayer 579* (JEPS).

1i. Streptanthus glandulosus subsp. **secundus** (Greene) Kruckeb., Madroño 14: 223. 1958. Basionym: *Streptanthus secundus* Greene, Fl. Fran. 261. 1891. *Euklisia secunda* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 83. 1904, as "*Euclisia*." TYPE: U.S.A. California: Marin Co., N base, Mt. Tamalpais, 18 May 1886, *E. L. Greene s.n.* (holotype, NDG not seen).

Distribution and habitat. *Streptanthus glandulosus* subsp. *secundus* is uncommon in Marin County, limited to the north slopes of Mount Tamalpais and adjacent Lucas Valley in California (Appendix 1).

Discussion. Inflorescences of *Streptanthus glandulosus* subsp. *secundus* are secund and perianths are cream to light greenish yellow with rose or lavender-purple on sepal base or petal veins.

1j. Streptanthus glandulosus subsp. **sonomensis** (Kruckeb.) M. S. Mayer & D. W. Taylor, Novon 18: 280. 2008. Basionym: *Streptanthus glandulosus* var. *sonomensis* Kruckeb., Madroño 14: 223. 1958. TYPE: U.S.A. California: Sonoma Co., near Guerneville, Great Eastern Quicksilver Mine, serpentine, 8 June 1948, *F. W. Hoffman 2323* (holotype, UC!; isotypes, GH not seen, MO!).

Distribution and habitat. *Streptanthus glandulosus* subsp. *sonomensis* is uncommon and is found predominantly on serpentine soils in Sonoma County, California (Appendix 1).

Discussion. Inflorescences of *Streptanthus glandulosus* subsp. *sonomensis* are typically secund, sepals are pale yellow, white, or greenish white, and petals are white. This subspecies lacks the reddish or purple coloring of the sepal base and veins shown by *S. glandulosus* subsp. *secundus*, which occurs in Marin County.

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APPENDIX 1. Voucher information for specimens used in analysis of ITS phylogeny. All specimens were collected in California and are deposited at JEPS unless otherwise noted in parentheses. Clade terminal (Fig. 1) and GenBank accession numbers are noted in brackets. Asterisks note sequences previously analyzed (Mayer & Soltis, 1999).

Streptanthus glandulosus subsp. *albidus*. U.S.A. **California:** Santa Clara Co., E of Coyote, *M. Mayer 584* [584.4, DQ829790].

Streptanthus glandulosus subsp. *arkii*. U.S.A. **California:** Colusa Co., Wilbur Hot Springs, Wilbur Springs Rd., *R. Raiche 105* [105.4, DQ829797]; Napa Co., Pope Valley Rd., *M. Mayer 563* [563.4, DQ829799]; Lake Hennesy, Hwy. 128 roadside SE of dam, *M. Mayer 573* [573, ITS-1: AF111405*, ITS-2: AF111406*]; Solano Co., Weldon Canyon Rd., *M. Mayer 561* [561, ITS-1: AF111351*, ITS-2: AF111352*]; *M. Mayer 562* [562.4, DQ829800].

Streptanthus glandulosus subsp. *glandulosus*. U.S.A. **California:** Alameda Co., Sunol Reg. Wilderness, above Alameda Creek, *R. Raiche 306* [306, EF208035]; 1 km up creek adj. to W parking lot, *M. Mayer 582* [582.4, DQ829804]; Contra Costa Co., Mt. Diablo State Park, N Gate Rd., *M. Mayer 581* [581.4, DQ829792]; San Benito Co., Panoche Rd., 19 km S of Hwy. 25, *M. Mayer 564* [564.4, DQ829796]; San Luis Obispo Co., Santa Rosa Creek Rd., *M. Mayer 556* [556.4, DQ829785]; Santa Clara Co., Santa Teresa Hills, Calero Reservoir, *R. Raiche 303* [303.4, DQ829784]; Mt. Hamilton, W of Lick Observatory, *M. Mayer 583* [583.4, DQ829791]; Morgan Hills, Glen Ayre Rd., *M. Mayer 585* [585.4, DQ829798]; Henry Coe State Park, Corral Trail, *M. Mayer 587* [587.4, DQ829786].

Streptanthus glandulosus subsp. *hoffmanii*. U.S.A. **California:** Sonoma Co., E ridge of The Cedars Canyon, *M. Mayer 548* [548.4, DQ829802].

Streptanthus glandulosus subsp. *niger*. U.S.A. **California:** Marin Co., Tiburon Peninsula, SE of end of Mira Flores Ln., *M. Mayer 535* [535.4, DQ829783]; Tiburon Peninsula, slopes beside St. Hillary's Church, *M. Mayer 536* [536, ITS-1: AF111393*, ITS-2: AF111394*].

Streptanthus glandulosus subsp. *pulchellus*. U.S.A. **California:** Marin Co., Mt. Tamalpais, Bootjack Camp, *M. Mayer 537* [537.4, DQ829787]; Mt. Tamalpais, Carson Ridge, Pine Mtn. Trail, *M. Mayer 539* [539.4, DQ829788].

Streptanthus glandulosus subsp. *raichei*. U.S.A. **California:** Mendocino Co., Covelo Rd., 30 km E of Hwy. 101, *M. Mayer 557* [557.4, DQ829795]; Feliz Creek Rd., W of Hopland, *M. Mayer 565* [565.4, DQ829794]; Mountain House Rd., N of Hwy. 128, *M. Mayer 569* [569, ITS-1: AF111397*, ITS-2: AF111398*]; Sonoma Co., Pine Flat Rd., N of Hwy. 128, *M. Mayer 579* [579.4, DQ829793].

Streptanthus glandulosus subsp. *secundus*. U.S.A. **California:** Marin Co., Woodgate, 1 km NW of San Geronimo Ridge, *M. Mayer 542* [542, ITS-1: AF111381*, ITS-2: AF111382*]; E end of Lucas Valley, *M. Mayer 543* [543.4, DQ829789].

Streptanthus glandulosus subsp. *sonomensis*. U.S.A. **California:** Sonoma Co., Bohemian Hwy., at crossing with Duvoul Creek, *M. Mayer 545* [545.4, DQ829803]; rd. to The Cedars, 1 km E of crossing of Big Austin Creek, *M. Mayer 546* [546, EF208036]; Guerneville, E of summit of Sweetwater Springs Rd., *M. Mayer 549* [549.4, DQ829801].

Streptanthus polygaloides, outgroup. [AF111419, AF111420] (Mayer & Soltis, 1999).